Current Zoology 58 (4): 620–629, 2012

How spiders practice aggressive and Batesian mimicry

Ximena J. NELSON[1*], Robert R. JACKSON[1,2]

[1] School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

[2] International Centre of Insect Physiology and Ecology, Thomas Odhiambo Campus, P.O. Box 30 Mbita Point, Kenya

Abstract To understand communication, the interests of the sender and the receiver/s of signals should be considered separately. When our goal is to understand the adaptive significance of specific responses to specific signals by the receiver, questions about signal information are useful. However, when our goal is to understand the adaptive significance to the sender of generating a signal, it may be better to envisage the receiver's response to signals as part of the sender's extended phenotype. By making signals, a sender interfaces with the receiver's model of the world and indirectly manipulates its behaviour. This is especially clear in cases of mimicry, where animals use deceptive signals that indirectly manipulate the behaviour of receivers. Many animals adopt Batesian mimicry to deceive their predators, or aggressive mimicry to deceive their prey. We review examples from the literature on spiders to illustrate how these phenomena, traditionally thought of as distinct, can become entangled in a web of lies [*Current Zoology* 58 (4): 620–629, 2012].

Keywords Mimicry, Communication, Spider, Deception, Signal, Search image

1 (Mis)communication and Mimicry

An understanding of mimicry has ramifications in sensory biology, animal cognition and animal communication. Much of animal communication is viewed as essentially cooperative information sharing in which, to varying degrees, the interests of the sender and the receiver are mutually compatible (Searcy and Nowicki, 2005). In contrast, mimicry is primarily based on deception, with aggressive mimics being predators that deceive their prey and Batesian mimics being prey that deceive their predators. The ambiguous exception to this is Müllerian mimicry, where noxious animals advertise their unpalatability and resemble each other, but differ in their level of noxiousness - and hence in their deceitfulness (Ruxton et al., 2004). The phenomena of Batesian and aggressive mimicry are certainly not cooperative, but we can avoid the emphasis on mutually compatible interests by characterising communication as being fundamentally about indirect manipulation of behaviour, as suggested by Dawkins and Krebs (Dawkins and Krebs, 1978; Krebs and Dawkins, 1984).

Communication requires a network consisting of signals and at least two players, a sender and a receiver of the signals. We can think of information as being a correlation, and identifying reliable correlations may go a long way toward explaining how and why the receiver responds to a signal. With aggressive and Batesian mimicry, we can substitute the term 'misinformation' to denote deception.

The term 'mimicry' implies that we can specify a model, with our perception of what the model signifies to the deceived party corresponding roughly to what we mean by misinformation. Information (or misinformation) is relevant when trying to explain the receiver's response, but is some steps removed when trying to explain why the mimic deploys particular signals. This is because to understand the adaptive significance of signals for the sender, what matters is that the receiver's response to the signal is part of the sender's extended phenotype (Dawkins, 1982).

Although making fine distinctions and having different terms for specifying them can be useful, the literature on mimicry and communication sometimes appears to be sinking under the terminological load, which includes 'sensory traps', 'sensory exploitation', 'sensory drive', 'receiver psychology', and 'exploitation of perceptual biases' (Christy, 1995; Bradbury and Vehrencamp, 1998; Endler and Basolo, 1998; Jabłoński, 2001; Ruxton et al., 2004; Schaefer and Ruxton, 2009). We will attempt to avoid excessive jargon in this review, in part because real-world examples often seem to defy our efforts to define and label discrete categories and it is especially these messier examples that interest us here.

Received Nov. 18, 2011; accepted Jan. 14, 2012.

* Corresponding author. E-mail: ximena.nelson@canterbury.ac.nz

2 Aggressive Mimicry and *Femmes Fatales*

Using examples of aggressive mimicry in angler fish, Dawkins and Krebs (1978) illustrated why their perspective on communication emphasized manipulation instead of information. Angler fish prey on smaller fish, which in turn prey on small invertebrates. The angler fish's aggressive-mimicry signal comes from twitching a fleshy spine that extends in front of its mouth. When the small fish responds and approaches, it is eaten by the angler fish. Using the expression 'misinformation' is a convenient way of acknowledging a straightforward explanation of the small fish's response but questions about information (or misinformation) do not clearly explain why the angler fish makes the signal. We can say that the small fish is expressing a predisposition to respond in a particular way to the mimic's stimulus because the occurrence of this stimulus is normally correlated with the presence of the small fish's prey (Wilson, 1937; Pietsh and Grobecker, 1978). It is the small fish's misfortune that its last response leads it to a predatory angler fish, but aggressive mimicry works because things usually do not go wrong for the receiver.

Specifying a precise model mimicked by the angler fish appears to be easy, and comparable precision is evident for two spider *femmes fatales*. The first are bolas spiders, these being spiders that specialize at eating male moths (Eberhard, 1977; Stowe et al., 1987; Yeargan, 1994). Female moths typically attract conspecific males by releasing sex pheromones. The male moth detects the pheromone, flies upwind and finds the female. At night, bolas spiders hunt moths by using a single line of silk with a drop of sticky glue on the distal end. They swing this so-called 'bolas' around and the male moth ends up stuck to the glue drop. The bolas spider's ploy is to release a chemical cocktail that mimics the female moth's pheromones and then, when flying upwind as though to find a mating partner, the male is greeted instead by an arachnid *femme fatale*.

The other example is the predator *Portia fimbriata,* and its prey is *Euryattus* sp. Both are jumping spiders (Salticidae). *Euryattus* and most salticids do not build webs, but females of *Euryattus* build unusual nests. By using heavy silk guy lines, the female suspends a dead, rolled-up leaf from the vegetation or from a rock ledge (Jackson, 1985). The spatial acuity supported by salticid eyes sets them apart from other spiders (Land and Nilsson, 2002) and the *Euryattus* male uses his eyesight to identify a female's leaf nest. Once spotted, he walks slowly down a guy line, positions himself on the leaf and then, by suddenly flexing his legs, he violently shakes the leaf. This is his courtship signal. The female inside the nest does not see the male, but responds to the signal by coming out to mate if she is receptive or to drive him away if she is not. The *Euryattus* female's *femme fatale* is a *P. fimbriata* female that sees the suspended rolled-up leaf, moves down a guy line and positions herself close to and facing an opening to the rolled-up leaf. She then simulates the courtship signals normally made by *Euryattus* males (Jackson and Wilcox, 1990), but this time when the *Euryattus* female comes out in response to the signal, the suitor who greets her is instead a predator.

With both of these *femmes fatales*, we can say the model was a signal used in male-female interactions by a particular species. These examples are also cases of what we might call a narrow definition of aggressive mimicry, where the resemblance of harmless model allows the mimics to prey on the model itself. This may leave us with a satisfying impression of precision when talking about aggressive mimicry, and yet it is not clear why we should think taxonomic precision is particularly important. To understand why aggressive mimicry works it is the prey's classification system that matters, not formal scientific taxonomy. For this reason researchers now tend to adopt a broader view of aggressive mimicry whereby the mimic preys on the model or unsuspecting third parties undeterred by the harmless appearance of the approaching predator (e.g., Côté and Cheney, 2007)- a perspective that has the advantage of highlighting interesting issues related to sensory ecology and animal cognition.

3 Use of Behavioural Plasticity in Aggressive Mimicry

Portia's use of aggressive mimicry when preying on *Euryattus* females is only one expression of an active preference for spiders as prey (Harland and Jackson, 2004). *Portia* also invades the webs of non-salticid spiders and, when in another spider's web, explaining how *Portia*'s signals work is considerably less straightforward than in the *Portia*-*Euryattus* example. One of the first things we need to consider is the web-building spider's sensory system. We are predisposed to think of sense organs as being part of an animal's anatomy, but for web-building spiders, the web becomes, in conjunction with setae and slit sensilla on the spider's body, an

integral part of a critically important sense organ (Witt, 1975; Barth, 2001). This is a particularly interesting sense organ because, being extended out into the environment, it is a sensory system *Portia* can walk directly into, giving especially literal meaning to the expression 'sensory exploitation'. However, when *Portia* invades a web, it enters into intimate and often dangerous contact with its prey's sensory world - dangerous because the tables may be turned, and *Portia*'s intended dinner may well eat *Portia* instead.

Rather than simply stalking or chasing down the resident spider after entering the web, *Portia* encourages behaviour by the resident spider that is advantageous to *Portia* but to the undoing of the resident spider. *Portia* does this is by placing signals directly into the resident's sensory system (i.e., the web). Using any one or any combination of its ten appendages (eight legs and two palps) in combination with abdominal movements, *Portia* manipulates the web threads. Because each appendage can be moved independently and in a variety of ways *Portia* has at its disposal a virtually unlimited arsenal of different signals for deploying in other spiders' webs (Jackson and Wilcox, 1993; Tarsitano et al., 2000). This is useful because *Portia*, instead of targeting just a few web-building spiders, appears to be ready to take on almost any spider in a web as long as it is similar to its own size (Jackson and Blest, 1982).

Whether a particular web signal is significant to a resident spider varies depending on species, sex-age class, feeding state and previous experience. This presents *Portia* with a problem of how to select the particular signal that will work in a particular session with a particular resident spider. *Portia* solves this problem by being innately predisposed to begin with particular signalling routines during encounters with some of its more common natural prey and by initiating a trial-and-error routine when the prey is any other spider for which it does not have a pre-programmed tactic (Harland and Jackson, 2004). After entering the web of the latter type of spider, *Portia* begins by generating a kaleidoscope of different vibratory signals. When one of these signals eventually elicits an appropriate response from the resident, *Portia* stops varying its signals and instead concentrates on making the signal that worked (Jackson and Wilcox, 1993; Jackson and Nelson, 2011). This may sound simpler than it actually is because, although the resident spider may respond appropriately and although *Portia* may hone in on signals that work, there is no guarantee that the resident will continue to respond appropriately long enough for *Portia* to make a kill. If the resident spider switches to inappropriate behaviour, *Portia* finds another effective signal by reverting to trial-and-error. What makes a response 'appropriate'? Specifying this goes hand in hand with specifying the mimic's model. Yet from *Portia*'s perspective, no one response is always appropriate. When using trial-and-error, *Portia* appears to make decisions ahead of time regarding what will qualify as 'appropriate'.

When the resident spider is small and not especially dangerous, an appropriate response seems to be for the resident to behave as if *Portia*'s vibratory signal were coming from a small insect ensnared in the web. The resident spider approaches and, when close, *Portia* lunges to make the kill (Jackson and Blest, 1982). Here *Portia* seems to be joining the angler fish as a straightforward example of a predator practising aggressive mimicry by simulating the prey's own prey.

However, simulating a resident spider's own prey might be courting disaster when *Portia* enters the web of a large or otherwise dangerous spider because *Portia* might actually become the meal it pretends to be. *Portia*'s apparent solution is to adopt a different definition of 'appropriate'. Adjusting signals in response to feedback from the resident spider, *Portia* now avoids repeating signals that initiate what might become a full-scale attack. Sometimes success for *Portia* seems to be based on getting the powerful resident to approach slowly and hesitantly, as though uncertain of the identity of the signals received. Alternatively, *Portia* may make signals that keep the victim calm and stationary, while *Portia* stealthily moves in for the kill (Harland and Jackson, 2004).

With *Portia*, we have moved beyond aggressive mimicry where a mimic's model can be easily specified, yet we become aware of remarkable plasticity in a predator (Nelson and Jackson, 2011a). When in the web of a dangerous spider, *Portia*'s signals appear to assist prey capture (i.e., aggressive mimicry) and at the same time deter a predatory attack by the resident spider by providing appeasement signals.

4 Myrmecomorphy

The most thoroughly studied examples of spiders practising Batesian mimicry come from myrmecomorphic species, this being a term used for animals that, from a human perspective, look like ants. Myrmecomorphy evolved at least 50 million years ago among spiders (Wunderlich, 2000), and is currently expressed in at least 43 genera from 13 families (Cushing, 1997); a consequence of at least 70 instances of independent ori-

gins (McIver and Stonedahl, 1993). While we might misclassify a myrmecomorphic spider as being an ant, whether spider predators are deceived by myrmecomorphy requires experimental evidence. This is especially important because animal eyes vary considerably in their capacity for spatial acuity, colour vision and in the processing of information delivered by the eyes (Cuthill and Bennett, 1993; Gregory, 1998; Land and Nilsson, 2002).

There are especially many myrmecomorphic species from the family Salticidae (Cushing, 1997) and there is considerable evidence that ant-averse mantises and ant-averse salticids respond to the myrmecomorphic salticids as though they were ants (e.g., Cutler, 1991; Edmunds, 1993; Nelson and Jackson 2006a; Nelson et al., 2006a; Huang et al., 2011). These findings are evidence that these myrmecomorphic spiders are Batesian mimics of ants.

However, myrmecomorphic spiders differ from the classic examples of Batesian mimicry where the mimic is a palatable species that deceives predators by advertising like an aposematic prey species. Aposematic species are harmful or unpalatable and communicate this to potential predators, often through high contrast 'warning colours', such as reds and yellows (Joron and Mallet, 1998). 'Aposematic' might not be an appropriate label for most ants because, although ants have defences that repel many would-be predators and although their appearance is distinctive, it is unlikely that their slender body, narrow waist, erratic style of locomotion, and distinctive way of waving their antennae evolved as a mechanism by which ants warn predators of their ability to defend themselves. Yet, for the predator, hypotheses about the origin of the ant's general appearance are irrelevant.

There is a second unconventional aspect about the research on myrmecomorphic salticids, which is that the predator's aversion to ants is often innate (Nelson and Jackson, 2011b). Currently, there is a pervasive emphasis on learning as the mechanism by which predators acquire an aversion to aposematic models. Batesian mimics are then envisaged as exploiting the predator's learned aversion to the aposematic prey. Consistent with this emphasis, birds tend to be the predator of choice when thinking about Batesian mimicry. Birds have good eyesight (Land and Nilsson, 2002) and they certainly eat spiders (Bristowe, 1941; Gunnarson, 2007), yet we know remarkably little about the specific predators that impact significantly on spider populations in the field. More attention to predatory insects might be instructive, especially as it is known that some predatory insects specialize on spiders (Jackson et al., 2010; Wignall and Taylor, 2010). Predatory (or parasitoid) wasps (e.g., Edmunds, 1993; Blackledge et al., 2003; Araújo and Gonzaga, 2007; Polidori et al., 2007; Eberhard, 2010) are of particular interest because there may be many species from the wasp families Crabronidae and Sphecidae that exclusively target spiders. However, when addressing hypotheses about myrmecomorphy functioning as Batesian mimicry, the predators of interest are predators for which the specific appearance of the mimic is salient. This implies that our goal should be experiments in which we ensure the predator is relying on vision based on good spatial acuity, as it is good spatial acuity that renders visual objects rich in detail about static appearance (Land and Nilsson, 2002). Owing to the paucity of appropriate experiments, the relevance of predatory insects when addressing hypotheses about the evolution of myrmecomorphy remains uncertain.

Salticids have eyesight based on spatial acuity exceeding that known for other spiders or for any other animal in their size range (Land and Nilsson, 2002), making them particularly tractable for testing hypotheses about role of the prey's appearance in determining the predator's behaviour. For example, salticids can be tested with dead prey mounted in lifelike posture or with virtual prey rendered by computer animation (Nelson and Jackson, 2011a), enabling fine control over variables that would confound interpretation of findings when using living prey. Additionally, spiders with no experience with ants or mimics can be tested. This is important because of the heavy emphasis on learning in the literature on Batesian mimicry, which makes it easy to overlook the likely prevalence of cases of Batesian mimicry based on innate aversion (see Caldwell and Rubinoff, 1983; Caley and Schluter, 2003).

5 Deploying Batesian Mimicry of Ants in the Service of Obtaining Prey

Salticids are usually solitary hunters (Jackson and Pollard, 1996), but there are several species in the Lake Victoria region of Kenya and Uganda that build clusters of nests interconnected by silk ('nest complexes'). These nest complexes can be occupied by 50 or more individuals (Jackson, 1986). Several salticid species often share the same nest complex and ants are never far away. *Myrmarachne melanotarsa*, one of the species living in nest complexes, closely resembles an unidentified species of *Crematogaster* (Wesolowska and Salm,

2002) that is very common in the same habitat and this mimicry protects them from ant-averse predators (Nelson and Jackson, 2009a).

Crematogaster typically moves from place to place in columns, with *M. melanotarsa* often joining the marching ants, arriving at sources of honeydew and then feeding alongside the ants (Jackson et al., 2008). *Myrmarachne melanotarsa* also feeds on the eggs and small juveniles of the non-myrmecomorphic salticids in nest complexes and does so using 'collective mimicry' (Nelson and Jackson, 2009a). Females of the non-myrmecomorphic salticid species flee when a swarm of ants moves across a nest complex, and *M. melanotarsa* exploits these salticids' predisposition to flee from ants (Nelson and Jackson, 2009b).

When experiments were carried out using decoys made from dead ants and *M. melanotarsa*, the non-myrmecomorphic salticids living in nest complexes were especially prone to flee when they could see a group of *Crematogaster* or a group of *M. melanotarsa* in the vicinity, and not so prone to abandon nest complexes when all they could see was a single *Crematogaster* or a single *M. melanotarsa* (Nelson and Jackson, 2009a). Fleeing from a *Crematogaster* swarm might not be so bad, as the nest-complex silk and the silk around egg sacs usually suffice as barriers that keep eggs and small juveniles out of harm's way. However, being spiders, a swarm of *M. melanotarsa* has little difficulty negotiating the silk and preying on the unguarded brood. As a consequence, this Batesian mimic deploys a novel strategy for obtaining prey, whereby the resemblance to ants has enabled it to exploit a new trophic niche through the deterrence of the guardians of the brood of spiders. Unlike in examples of aggressive mimicry, here the effect of the signal on the receiver is not one of appeasement through resemblance of harmless prey, but one that produces precisely the opposite response, yet for the mimic the net result (obtaining prey through deceit) is the same.

6 Targeting Ants with Aggressive Mimicry

Most spiders may be averse to eating ants, but routine predation on ants is characteristic of a sizeable minority of species, some of which are myrmecomorphic (Pekár and Král, 2002). However, using the label 'aggressive mimicry' solely on the basis of seeing myrmecomorphic spiders eat ants is highly misleading. Conclusions about aggressive mimicry specifically require evidence that the prey is deceived. In most instances, it may be unlikely that myrmecomorphy deceives ants, as ants are better known for their strong reliance on chemoreception instead of vision when identifying prey, predators and other ants (Hölldobler and Wilson, 1990).

Many ants rely on cuticular hydrocarbons to distinguish between nestmates and aliens (Howard and Blomquist, 2005; Hefetz, 2007). That spiders can exploit these chemical-identification systems is exemplified by *Cosmophasis bitaeniata*, a salticid from Australia that acquires the cuticular hydrocarbons used by weaver ants *Oecophylla smaragdina*. Chemically disguised as a weaver ant, this salticid enters the ant's nest, where it feeds unmolested on the ant's eggs and larvae (Allan et al., 2002; Elgar and Allan, 2004). This species is the most thoroughly studied example of a spider using aggressive mimicry targeted at ants, but in this instance aggressive mimicry is based on chemoreception.

Cosmosphasis bitaeniata, like the bolas spider, is a predator that relies on chemical signals when deceiving its prey, with *C. bitaeniata* pretending to be an ant and the bolas spider pretending to be a female moth. Both of these predators communicate with their prey, but they use signals in strikingly different ways. The bolas spider elicits a specific overt response from its prey (i.e., flying upwind toward the spider), but *C. bitaeniata* seems to be doing the opposite. Instead of an evoking an overt response by the ant, *C. bitaeniata*'s strategy appears to be based on ensuring that the ant remains passive.

7 The Web-Like Nature of the Categories of Mimicry

With spiders, aggressive and Batesian mimicry relate to a diversity of traits and often these two categories seem to be entangled. Signals from a bolas spider manipulate the behaviour of the organism it will eat (the male moth), but signals from *C. bitaeniata*, by ensuring that the ant remains passive instead of responding overtly, manipulate not the animals *C. bitaeniata* will eat (the ants' brood) but instead their guardians. As such, *C. bitaeniata* is similar to *M. melanotarsa*, which also manipulates the behaviour of the guardians of its intended prey, not the prospective prey organisms themselves. However, *M. melanotarsa* is like the bolas spider, and unlike *C. bitaeniata*, because its strategy is to provoke a specific overt response by the guardian. Finally, *M. melanotarsa* differs from both by deploying Batesian mimicry in the service of obtaining prey.

It has been suggested that the relationship between

model and the targeted receiver differs in an important way depending on whether we are considering aggressive or Batesian mimicry, with Batesian mimics inserting themselves into antagonistic predator-prey interactions and with aggressive mimics inserting themselves into cooperative interactions (Cheney and Côté, 2005). The basic idea is that Batesian mimics pretend to be something that would normally be harmful to would-be predators and aggressive mimics pretend to be something that would normally be useful to would-be prey. The antagonistic-cooperative distinction might be applicable in many instances, but *M. melanotarsa* may defy this distinction by using its mimicry to obtain prey through inserting itself itself into an antagonistic, instead of a cooperative, interaction with the guardians of its prey (Nelson and Jackson, 2009b). The general lesson seems to be that, despite the way our terms make us expect discrete categories with tidy boundaries, a continuum and entangled categories are often a more realistic expectation.

8 Sexually Dimorphic Ant Mimics

Besides being strikingly myrmecomorphic, the species from the genus *Myrmarachne* express conspicuous sexual dimorphism. Unlike the female's chelicerae, which are angled downward and not especially large, the male's chelicerae are enormous appendages (Fig. 1A) that may extend forward almost as far as the body extends to the rear (Pollard, 1994; Edwards and Benjamin, 2009). Male-male competition for access to mating partners is probably the primary context in which males evolved these fantastic chelicerae. Males compete with each other for access to females using threat displays in which the chelicerae are spread apart and the long, sabre-like, fangs are extended (Figs. 1B, 2) prior to wrestling (Nelson and Jackson, 2007).

Fig. 1 Displaying ant mimics
A. *Myrmarachne bakeri* female (left) facing courting male (right). **B**. Two *Myrmarachne assimilis* males (mimics of the Asian weaver ant *Oecophylla smaragdina*) engaged in aggressive displays. Note long chelicerae of males.

Carrying around massive chelicerae might seem antithetical to retaining myrmecomorphy, but this is a misleading hunch. In experiments, predators that avoid ants and *Myrmarachne* females also avoid *Myrmarachne* males. The hypothesis supported by experimental evidence is that, instead of resembling a single ant, a male resembles an ant that is carrying something, such as another ant, in its chelicerae (an 'encumbered ant') (Fig. 3). The strongest evidence comes from using not ant-averse predators, but instead myrmecophagic salti-

Fig. 2 *Myrmarachne plataleoides* (mimic of the Asian weaver ant *Oecophylla smaragdina*) male
Threat display directed at another male. Palps held erected to the sides. Abdomen elevated. Chelicerae spread apart, with fangs extended. Note eye spots on chelicerae at articulation of fangs with basal segments.

cids (i.e., salticids that have an active preference for ants as prey). The myrmecophagic salticids' preferred ants are encumbered ants (possibly because their dangerous jaws are already busy), and they express a preference for *Myrmarachne* males as though these myrmecomorphic salticids were encumbered ants (Nelson and Jackson, 2006b).

Mimicking an ant carrying something else has been called 'compound mimicry' and *Myrmarachne* males, by adopting compound mimicry, have apparently solved the problem of how to take sexual dimorphism to an extreme without jeopardizing myrmecomorphy, but at the cost of attracting the unwanted attentions of myrmecophagic predators (Nelson et al., 2006b).

In Sri Lanka, *Myrmarachne plataleoides* (Fig. 2) is an especially precise mimic of *Oecophylla smaragdina* and the males adopt a refined version of compound mimicry. There is a black spot positioned on the top of the distal end of the basal segment of each of the male's chelicerae (Wanless, 1978). Weaver ant colonies have major workers that forage and minor workers that care for the eggs and larvae inside the nest (Crozier et al., 2010). Major workers commonly carry minors from one sub-nest to another by holding the smaller ant's abdomen in their mandibles. While being carried, the minor worker holds its legs against the side of its body and *M. plataleoides* males, with 'eyespots' on their long chelicerae, are remarkably similar in appearance to these worker-ant duos.

Fig. 3 Compound mimicry by male *Myrmarachne*
A. Major worker of the Australian weaver ant, *Oecophylla smaragdina*, carrying a minor worker in its mandibles. **B**. Male *Myrmarachne smaragdina* in sparsely woven nest. Note: long chelicerae resemble the minor worker being carried by ant (see (a)). Photo: Sara Ceccarelli.

9 Diversification as A Key to Success among Mimics

Compound mimicry linked to sexual dimorphism (Fig. 3) implies that, for all *Myrmarachne* species, at least two models need to be specified when characterizing how ant mimicry is expressed, an ant and an encumbered ant. Transformational mimicry may also be widespread in myrmecomorphic spiders, this being a term for instances of different size classes during individual ontogeny adopting different models, with the model adopted being an ant of comparable body size (Reiskind, 1970). However, even same sex and same size individuals within a single species sometimes differ considerably in appearance and adopt different models (Edmunds, 1978; Wanless, 1978; Borges et al., 2007; Ceccarelli and Crozier, 2007). Individuals of a species from the Philippines, *M. bakeri* (Fig. 1a), can change

morph even within a single instar (Nelson, 2010).

The selection pressures responsible for the prevalence of polymorphism among myrmecomorphic spiders may be poorly understood, but hypotheses regarding why camouflaged prey are often polymorphic might be, with modification, applicable to Batesian mimics. When prey is camouflaged, predators often feed selectively on the more common morphs, with selective predation being mediated by the predator deploying a search image against prey that exceed a threshold in abundance. The resulting frequency dependent selection favouring rare morphs has been shown experimentally to generate polymorphism (Bond and Kamil, 1998, 2002). Being the expression of selective attention, not a shift in preference, search images are fundamentally cognitive, and polymorphism can be envisaged as a consequence of camouflaged prey exploiting the predator's limited capacity for selective attention (Bond, 2007; Shettleworth, 2009).

Limited capacity for selective attention might also mediate the evolution of polymorphism by Batesian mimics. Rare mimic morphs may deceive predators, including invertebrates, that become attentive to morphs exceeding a threshold in abundance. Although the tradition has been to use vertebrates as the predators in search-image research, wasps (Ishii and Shimada, 2010) and also salticids are known to adopt search images, and salticids are also subject to limited capacity for selective attention (Jackson and Cross, 2011). We are currently investigating *Portia*'s capacity to identify myrmecomorphic spiders as prey instead of ants, and to deploy search images and thereby prey selectively on morphs that become common.

10 Conclusion

In this review we have attempted to highlight the complexity of mimicry as a note of caution to researchers, including ourselves, in this field. The first point to make is that we should refrain from thinking that mimicry is selected for purely through learned mechanisms on the part of the predator, but can also be selected by innate aversion (Caldwell and Rubinoff, 1983; Caley and Schluter, 2003; Nelson and Jackson, 2011b). The ramifications for the mimic, whether aversion is learned or innate, are probably quite similar, but the effects on the predator in these two cases differ considerably. Consequently, research in this area will be especially instructive in elucidating the selective agents for mimicry. The second major point we raise, related to the first, is that selection can be multifaceted, and need not be due to a single 'cause'. Selection for Batesian mimicry may arise due to a multitude of different predators, some using learned aversion and others using innate aversion, but may also provide new opportunities for the mimic (such as opening up new trophic niches in the case of *Myrmarachne melanotarsa*) which may enhance the selection pressure for accurate resemblance to the model. It seems singularly unlikely that selection for traits boils down to one specific channel, as can be seen in the interplay between sexual selection and natural selection, here exemplified by male *Myrmarachne*. Finally, we suggest that in order to fully grasp the intricacy of mimicry in all is wonderful manifestations, both a firm knowledge of the natural history of the animal in question (for example, what the real-world predators of the mimics actually are) and experiments based on this knowledge, rather than assumptions, are required. For example, it is highly likely that our poor sense of smell and good eyesight has led us to describe a multitude of examples of visual resemblance of models, with an unlikely paucity of chemical mimics. Good fieldwork opens up the ground to explore other avenues of mimicry, as seen in the case of *Cosmophasis bitiaenta*. All too often we assume we know the model because of what the mimic resembles to our sensory systems, without testing these assumptions on the receivers themselves. Nature has a knack for adopting solutions that appear common sense in hindsight.

Acknowledgements We are grateful to Roy Snelling for helping us identify ants and to Bert Barrion and G.B. Edwards for helping us identify spiders. We thank Sara Ceccarelli for providing a photo of *Myrmarachne smaragdina*. We also gratefully acknowledge support of grants from the National Geographic Society and the Royal Society of New Zealand.

References

Allan RA, Capon RJ, Brown WV, Elgar MA, 2002. Mimicry of host cuticular hydrocarbons by salticid spider *Cosmophasis bitaeniata* that preys on larvae of tree ants *Oecophylla smaragdina*. J. Chem. Ecol. 28: 835–848.

Araújo MS, Gonzaga MO, 2007. Individual specialization in the hunting wasp *Trypoxylon* (*Trypargilum*) *albonigrum* (Hymenoptera, Crabronidae). Behav. Ecol. Sociobiol. 61: 1855–1863.

Barth FG, 2001. A Spider's World: Senses and Behavior. Berlin: Springer-Verlag.

Blackledge TA, Coddington JA, Gillespie RG, 2003. Are three-dimensional spider webs defensive adaptations? Ecol. Lett. 6: 13–18.

Bond AB, 2007. The evolution of color polymorphism: Crypticity searching images, and apostatic selection. Annu. Rev. Ecol. Evol. Syst. 38: 489–514.

Bond AB, Kamil AC, 1998. Apostatic selection by blue jays pro-

duces balanced polymorphism in virtual prey. Nature 395: 594–596.

Bond AB, Kamil AC, 2002. Visual predators select for crypticity and polymorphism in virtual prey. Nature 415: 609–613.

Borges RM, Ahmed S, Prabhu CV, 2007. Male ant-mimicking salticid spiders discriminate between retreat silks of sympatric females: Implications for pre-mating reproductive isolation. J. Insect Behav. 20: 389–402.

Bradbury JW, Vehrencamp SL, 1998. Principles of Animal Communication. Sunderland, MA: Sinauer Associates.

Bristowe WS, 1941. The Comity of Spiders. No. 128. London: The Ray Society.

Caldwell GS, Rubinoff RW, 1983. Avoidance of venomous sea snakes by naive herons and egrets. Auk 100: 195–198.

Caley MJ, Schluter D, 2003. Predators favour mimicry in a tropical reef fish. Proc. Roy. Soc. Lond. B 270: 667–672.

Ceccarelli FS, Crozier RH, 2007. Dynamics of the evolution of Batesian mimicry: Molecular phylogenetic analysis of ant-mimicking *Myrmarachne* (Araneae: Salticidae) species and their ant models. J. Evol. Biol. 20: 286–295.

Cheney KL, Côté IM, 2005. Frequency-dependent success of aggressive mimics in a cleaning symbiosis. Proc. Roy. Soc. Lond. B 272: 2635–2639.

Christy JH, 1995. Mimicry, mate choice, and the sensory trap hypothesis. Am. Nat. 146: 171–181.

Côté IM, Cheney KL, 2007. A protective function for aggressive mimicry? Proc. Roy. Soc. B 274: 2445–2448.

Crozier RH, Newey PS, Schluns EA, Robson SKA, 2010. A masterpiece of evolution – *Oecophylla* weaver ants (Hymenoptera: Formicidae). Myrmec. News 13: 57–71.

Cushing PE, 1997. Myrmecomorphy and myrmecophily in spiders: A review. Fla. Entomol. 80: 165–193.

Cuthill IC, Bennett ATD, 1993. Mimicry and the eye of the beholder. Proc. Roy. Soc. B 253: 203–204.

Cutler B, 1991. Reduced predation on the antlike jumping spider *Synageles occidentalis* (Araneae: Salticidae). J. Insect Behav. 4: 401–407.

Dawkins R, 1982. The Extended Phenotype. Oxford: Freeman.

Dawkins R, Krebs JR, 1978. Animal signals: Information or manipulation? In: Krebs JR, Davies NB ed. Behavioural Ecology: An evolutionary Approach. Oxford: Blackwell Scientific, 282–309.

Eberhard WG, 1977. Aggressive chemical mimicry by a bolas spider. Science 198: 1173–1175.

Eberhard WG, 2010. Recovery of spiders from the effects of parasitic wasps: Implications for fine-tuned mechanisms of manipulation. Anim. Behav. 79: 375–383.

Edmunds ME, 1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. Bull. Br. Arachnol. Soc. 4: 149–160.

Edmunds ME, 1993. Does mimicry of ants reduce predation by wasps on salticid spiders? Mem. Queensland Mus. 33: 507–512.

Edwards GB, Benjamin SP, 2009. A first look at the phylogeny of the Myrmarachninae, with rediscovery and redescription of the type species of *Myrmarachne* (Araneae: Salticidae). Zootaxa: 1–29.

Elgar MA, Allan RA, 2004. Predatory spider mimics acquire colony-specific cuticular hydrocarbons from their ant model prey. Naturwissenschaften 91: 143–147.

Endler JA, Basolo AL, 1998. Sensory ecology, receiver biases and sexual selection. Trends Ecol. Evol. 13: 415–420.

Gregory RL, 1998. Eye and brain: The psychology of seeing. 5th edn. Oxford: Oxford University Press.

Gunnarsson B, 2007. Bird predation on spiders: Ecological mechanisms and evolutionary consequences. J. Arachnol. 35: 509–529.

Harland DP, Jackson RR, 2004. *Portia* Perceptions: The umwelt of an araneophagic jumping spider. In: Prete FR ed. Complex Worlds from Simpler Nervous Systems. Cambridge: MIT press, 5–40.

Hefetz A, 2007. The evolution of hydrocarbon pheromone parsimony in ants (Hymenoptera: Formicidae) – interplay of colony odour uniformity and odor idiosyncrasy: A review. Myrmec. News 10: 59–68.

Hölldobler B, Wilson EO, 1990. The Ants. Heidelberg: Springer-Verlag.

Howard RW, Blomquist GJ, 2005. Ecological, behavioral, and biochemical aspects of insect hydrocarbons. Annu. Rev. Entomol. 50: 371–393.

Huang JN, Cheng RC, Li D, Tso IM, 2011. Salticid predation as one potential driving force of ant mimicry in jumping spiders. Proc. Roy. Soc. B 278: 1356–1364.

Ishii Y, Shimada M, 2010. The effect of learning and search images on predator-prey interactions. Popul. Ecol. 52: 27–35.

Jabłoński PG, 2001. Sensory exploitation of prey: Manipulation of the initial direction of prey escapes by a conspicuous 'rare enemy'. Proc. Roy. Soc. B 208: 1017–1022.

Jackson RR, 1985. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae, Salticidae) from Queensland: Utilization of silk, predatory behaviour, and intraspecific interactions. J. Zool. B 1: 145–173.

Jackson RR, 1986. Communal jumping spiders (Araneae: Salticidae) from Kenya: Interspecific nest complexes, cohabitation with web-building spiders, and interspecific interactions. N. Z. J. Zool. 13: 13–26.

Jackson RR, Blest AD, 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: Utilization of webs and predatory versatility. J. Zool. 196: 255–293.

Jackson RR, Cross FR. 2011. Spider cognition. Adv. Insect Physiol. 41: 115–174.

Jackson RR, Nelson XJ, 2011. Reliance on trial and error signal derivation by *Portia africana*, an araneophagic jumping spider from East Africa. J. Ethol. 29: 301–307.

Jackson RR, Nelson XJ, Salm K, 2008. The natural history of *Myrmarachne melanotarsa*, a social ant-mimicking jumping spider. N. Z. J. Zool. 35: 225–235.

Jackson RR, Pollard SD, 1996. Predatory behavior of jumping spiders. Annu. Rev. Entomol. 41: 287–308.

Jackson RR, Salm K, Nelson XJ, 2010. Specialized prey selection behavior of two East African assassin bugs, *Scipinnia repax* and *Nagusta* sp. that prey on social jumping spiders. J. Insect Sci. 10.

Jackson RR, Wilcox RS, 1990. Aggressive mimicry, prey-specific predatory behaviour and predator recognition in the predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Behav. Ecol. Sociobiol. 26: 111–119.

Jackson RR, Wilcox RS, 1993. Spider flexibly chooses aggressive mimicry signals for different prey by trial and error. Behaviour 127: 21–36.

Joron M, Mallet JLB, 1998. Diversity in mimicry: Paradox or paradigm? Trends Ecol. Evol. 13: 461–466.

Krebs JR, Dawkins R, 1984. Animal signals: Mind-reading and manipulation. In: Krebs JR, Davies NB ed. Behavioural Ecology: An Evolutionary Approach. Oxford: Blackwell Scientific, 380–402.

Land MF, Nilsson DE, 2002. Animal Eyes. Oxford: Oxford University Press.

McIver JD, Stonedahl G, 1993. Myrmecomorphy: Morphological and behavioral mimicry of ants. Annu. Rev. Entomol. 38: 351–379.

Nelson XJ, 2010. Polymorphism in an ant mimicking jumping spider. J. Arachnol. 38: 139–141.

Nelson XJ, Jackson RR, 2006a. Vision-based innate aversion to ants and ant mimics. Behav. Ecol. 17: 676–681.

Nelson XJ, Jackson RR, 2006b. Compound mimicry and trading predators by the males of sexually dimorphic Batesian mimics. Proc. Roy. Soc. B 273: 367–372.

Nelson XJ, Jackson RR, 2007. Complex display behaviour during the intraspecific interactions of myrmecomorphic jumping spiders (Araneae, Salticidae). J. Nat. Hist. 41: 1659–1678.

Nelson XJ, Jackson RR, 2009a. Collective Batesian mimicry of ant groups by aggregating spiders. Anim. Behav. 78:123–129.

Nelson XJ, Jackson RR, 2009b. Aggressive use of Batesian mimicry by an ant-like jumping spider. Biol. Lett. 5: 755–757.

Nelson XJ, Jackson RR 2011a. Flexibility in the foraging strategies of spiders In: Herberstein ME ed. Spider behaviour: Flexibility and Versatility. Cambridge: Cambridge University Press, 31–56.

Nelson XJ, Jackson RR 2011b. Use of flexible anti-predator ploys by spiders In: Herberstein ME eds. Spider behaviour: Flexibility and versatility. Cambridge: Cambridge University Press, 99–126.

Nelson XJ, Li D, Jackson RR, 2006b. Out of the frying pan and into the fire: A novel trade-off for Batesian mimics. Ethology 112: 270–277.

Nelson XJ, Jackson RR, Li D, Barrion AT, Edwards GB, 2006a. Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: Experimental findings from mantises (Mantodea). Biol. J. Linn. Soc. 88: 23–32.

Pekár S, Král J, 2002. Mimicry complex in two central European zodariid spiders (Araneae: Zodariidae): How Zodarion deceives ants. Biol. J. Linn. Soc. 75: 517–532.

Pietsch TW, Grobecker DB, 1978. The compleat angler: Aggressive mimicry in an antennariid anglerfish. Science 201: 369–70.

Polidori C, Federici M, Pesarini C, Andrietti F, 2007. Factors affecting spider prey selection by *Sceliphron* mud-dauber wasps (Hymenoptera : Sphecidae) in northern Italy. Anim. Biol. 57: 11–28.

Pollard SD, 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae). J. Zool. 234: 203–208.

Reiskind J, 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169: 587–588.

Ruxton G, Sherratt T, Speed M, 2004. Avoiding attack: The evolutionary ecology of crypsis, warning signals and mimicry. Oxford: Oxford University Press.

Schaefer HM, Ruxton GD, 2009. Deception in plants: Mimicry or perceptual exploitation? Trends Ecol. Evol. 24: 676–685.

Searcy WA, Nowicki S, 2005. The evolution of animal communication: Reliability and deception in signaling systems. Princeton, New Jersey: Princeton University Press.

Shettleworth SJ, 2009. Cognition, Evolution, and Behavior. 2nd edn. New York: Oxford University Press.

Stowe MK, Tumlinson JH, Heath RR, 1987. Chemical mimicry-bolas spiders emit components of moth prey species sex pheromones. Science 236: 964–967.

Tarsitano MS, Jackson RR, Kirchner W, 2000. Signals and signal choices made by araneophagic jumping spiders while hunting the orb-weaving spiders *Zygiella x-notata* and *Zosis geniculari*s. *Ethology* 106: 595–615.

Wanless FR, 1978. A revision of the spider genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian region. Bull. British Mus. Nat. Hist. 33: 1–139.

Wesolowska W, Salm K, 2002. A new species of *Myrmarachne* from Kenya. Genus 13: 409–415.

Wignall AE, Taylor PW, 2010. Predatory behaviour of an araneophagic assassin bug. J. Ethol. 28: 437–445.

Wilson DP, 1937. The habits of the angler-fish *Lophius piscatorius* L. in the Plymouth Aquarium. J. Mar. Biol. Assoc. 21: 477–497.

Witt PN, 1975. The web as a means of communication. Bioscience Comm. 1: 7–23.

Wunderlich J, 2000. Ant mimicry by spiders and spider-mite interactions preserved in Baltic amber (Arachnida: Acari, Araneae). European Arachnol. 2000: 355–358.

Yeargan KV, 1994. Biology of bolas spiders. Annu. Rev. Entomol. 39: 81–99.